An Anomaly in Potassium Accumulation by Barley Roots

II. EFFECT OF CALCIUM CONCENTRATION AND RUBIDIUM-86 LABELING

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ABSTRACT

When excised barley roots were incubated in 0.01 to 0.1 mM KCl solutions containing 0.2 mM CaSO₄, there was a peak in the K⁺ accumulation against concentration curve at 0.02 to 0.04 mM KCl. The peak in the K⁺ accumulation curve was shifted to lower K⁺ concentrations when Ca²⁺ concentration was decreased and to higher K⁺ concentrations when Ca²⁺ concentration was increased. Increasing Ca²⁺ concentration in the treatment solution was observed to be stimulatory, inhibitory, or neutral depending on the K⁺ concentration.

When ⁸⁶Rb was used as an isotopic tracer for K⁺, accumulation of K⁺ was grossly overestimated, and the apparent K⁺ accumulation curve, as estimated with ⁸⁶Rb-labeled K⁺, was hyperbolic over the concentration range of 0.01 to 0.1 mM. It was concluded that ⁸⁶Rb is a poor tracer for K⁺ over the concentration range of 0.01 to 0.1 mM. Accumulation of Rb⁺ in the presence of K⁺ was accurately measured by ⁸⁶Rb.

MATERIALS AND METHODS

Effect of Ca²⁺ Concentration. In previously reported studies of K⁺ accumulation from solutions of 0.01 to 0.1 mM K⁺, the treatment solutions always contained 0.2 mM CaSO₄ (8, 9). Figure 1 shows the results of a 0.1 mM KCl-NaCl replacement series experiment in which CaSO₄ was omitted. Accumulation curves for high K⁺-low Na⁺ solutions were not changed markedly by the omission of Ca²⁺ (compare with Fig. 1 of Ref. 9); however, omission of Ca²⁺ from low K⁺-high Na⁺ solutions strikingly reduced the apparent preference for K⁺ over Na⁺. In the absence of Ca²⁺ the peak of the K⁺ accumulation curve occurred at 0.01 mM, and the roots actually lost K⁺ to solutions containing 0.02 mM K⁺ and 0.08 mM Na⁺.

Figure 2 shows the effect of Ca²⁺ concentration on K⁺ accumulation in 24 hr from KCl solutions varied in concentration from 0.005 to 0.2 mM. In the absence of Ca²⁺, K⁺ accumulation showed a peak at the lowest KCl concentration used (0.005 mM) and a trough at 0.015 mM. With KCl concentrations greater than 0.02 mM the K⁺ accumulation curve was hyperbolic. The peak in the K⁺ accumulation curve was shifted to higher K⁺ concentrations as the solution Ca²⁺ concentration was increased. Varying the Ca²⁺ concentration from 0.02 to 1.0 mM had little effect on K⁺ accumulation from KCl solutions greater than 0.1 mM.

Since the studies of Viets (17) on the stimulating effect of calcium on ion uptake, considerable attention has been given to the relationship of Ca²⁺ to ion uptake. The results have not always been consistent, with both reported stimulation and inhibition of K⁺ uptake by Ca²⁺; and the foregoing results might partially explain these observations. Part of the data from Figure 2 is plotted in a different manner in Figure 3. Figure 3, K⁺ accumulation from four levels of KCl is plotted against Ca²⁺ concentration. The lowest Ca²⁺ concentration was 0.02 mM. With a KCl concentration of 0.01 mM all Ca²⁺ concentrations greater than 0.02 mM were inhibitory. With 0.03 mM KCl the accumulation of K⁺ was maximal in the presence of 0.1 mM Ca²⁺; however, all Ca²⁺ concentrations were stimulatory when compared with 0.02 mM Ca²⁺. With 0.05 mM KCl there was first a decrease, then an increase, in K⁺ accumulation as Ca²⁺ concentration was increased. Calcium concentrations greater than 0.02 mM had little effect on K⁺ uptake from 0.1 mM KCl. Figures 2 and 3 show

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Two KCl concentrations were chosen, representing the peak (0.04 mM) and the trough (0.08 mM) in the K⁺ accumulation curve. The absorption of K⁺ with time was determined by flame photometric determination of K⁺ and by labeling K⁺ with ⁸⁶Rb (16 μC/m mole). Net absorption of K⁺ determined chemically was greater from 0.04 mM than from 0.08 mM KCl at all time intervals between 2 and 24 hr (Fig. 5). On the other hand, when ⁸⁶Rb was used as a tracer for K⁺, apparent K⁺ accumulation was always less from 0.04 than 0.08 mM KCl.

Figure 6 shows apparent absorption curves for ⁸⁶Rb-labeled K⁺ in experiments of 0.5-, 1-, and 4-hr duration. The results are similar to those obtained by Epstein and coworkers over short duration periods (5, 6). It is evident from Figures 4, 5, and 6 that the use of ⁸⁶Rb labeling of K⁺ results in an inaccurate estimation of K⁺ accumulation over these concentration ranges.

**Rubidium and KCl Replacement Series Experiments.**

Figure 7 shows the results of a RbCl-NaCl replacement series experiment in the concentration range of 0.01 to 0.1 mM. Rubidium behaves somewhat similarly to K⁺ in that Rb⁺ accumulation reaches a maximum value and then decreases at higher Rb⁺ concentrations. Endogenous K⁺ is lost from the roots. This figure should be interpreted with reservations since the high levels of Na⁺ and Rb⁺, coupled with low levels of K⁺ in the roots, could conceivably influence metabolism. It was noted that the roots lost some turgidity after 24 hr in these solutions.

The results of a KCl-RbCl replacement series experiment are given in Figure 8. Simultaneous experiments were conducted with

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**Fig. 1.** Ion accumulation in 24 hr from a 0.1 mM replacement series of KCl and NaCl in the absence of Ca.

**Fig. 2.** Potassium accumulation in 24 hr from 0.005 to 0.2 mM KCl with different concentrations of CaSO₄.

that in 24-hr experiments, within the range of 0.01 to 0.1 mM K⁺, Ca²⁺ may either enhance or decrease K⁺ absorption depending on the K⁺ concentration.

**Absorption of ⁸⁶Rb-labeled K⁺.** Replacement series experiments were conducted with ⁸⁶Rb-labeled K⁺ (25 μC/m mole of K) and unlabeled K⁺ in simultaneous experiments. The results, in Figure 4, indicate that apparent K⁺ accumulation as determined with ⁸⁶Rb diverges considerably from actual K⁺ accumulation. These experimental results indicate that the anomaly in K⁺ accumulation at 0.01 to 0.1 mM K⁺ is not apparent when ⁸⁶Rb is used as a tracer for K⁺.

It should be emphasized that the indicated accumulation of ⁸⁶Rb-labeled K⁺ is an apparent value and overestimates the actual accumulation of K⁺. It is likely that this high value is largely due to exchange of ⁸⁶Rb for endogenous cations. The initial K⁺ content of these roots was approximately 18 μeq/g.

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**Fig. 3.** Effect of Ca concentration on K accumulation in 24 hr from solutions of four different KCl concentrations.

**Fig. 4.** Accumulation of Na and Cl, accumulation of K as determined chemically, and apparent accumulation of K as estimated by ⁸⁶Rb-labeling (25 μC/m mole of K) in 24 hr from a 0.1 mM replacement series of KCl and NaCl. The solutions contained 0.2 mM CaSO₄.
enhance the accumulation of K+ at KCl concentrations. The level of Ca2+ in the treatment solution affected the level of K+ at which the accumulation peak occurred. The peak was apparent, but small in magnitude when Ca2+ was omitted. When Ca2+ concentration was increased, the peak shifted to higher K+ concentrations.

VIET (17) first showed that Ca2+ or other polyvalent ions may enhance the absorption of K+. Usually Ca2+ decreases the absorption of highly hydrated ions such as Li+ and Na+ (1, 7, 10, 11, 18, 19) and enhances absorption of less hydrated ions such as K+ or Rb+ (4, 11, 12, 14, 15, 19). On the other hand, Elzam and Hodges (3) reported Ca2+ inhibition of K+ absorption by maize roots, and Kahn and Hanson (12) reported that Ca2+ enhanced K+ absorption from 1 mM KCl by maize roots and depressed K+ absorption by soybean roots. Bange and Shammin-Dellaert (1) reported that steady state Rb+ absorption by barley roots was insensitive to the presence of Ca2+. Hooymans (10) reported that Ca2+ inhibited K+ absorption by barley roots from 0.01 mM K+ and enhanced absorption from 0.2 mM K+.

The results reported here agree with those of Hooymans (10) and indicate that Ca2+ may be stimulatory, inhibitory, or neutral, depending on the K+ and Ca2+ concentration. While these results illustrate why Ca2+ may not consistently stimulate or inhibit monovalent ion absorption, they do not clarify the mechanism by which Ca2+ exerts its effect.

When K+ was isotopically labeled with 86Rb, the 86Rb content of the roots increased hyperbolically as the 86Rb concentration of the solution increased; in fact, no evidence of an absorption peak was evident with 86Rb-labeled K+. Absorption of 86Rb grossly overestimated K absorption from 0.04 and 0.08 mM KCl at all

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incubation intervals from 2 to 24 hr. These data indicate that the estimation of K absorption with $^{86}\text{Rb}$ as a tracer can lead to significant errors, particularly in the concentration ranges used here. The overestimation of K accumulation when $^{86}\text{Rb}$ is used is probably due to exchange between the tracer-labeled treatment solution and endogenous $K^+$. Maas and Leggett (13) have recently pointed out that isotopic measurements can lead to significant errors in estimating K absorption in maize roots. In agreement with Maas and Leggett, absorption of $Rb^+$ in the presence of $K^+$ was accurately measured by $^{86}\text{Rb}$.

**LITERATURE CITED**


